

Carbon storage and long-term rate of accumulation in high-altitude Andean peatlands of Bolivia

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SUMMARY

- (1) The high-altitude (4,500+ m) Andean mountain range of north-western Bolivia contains many peatlands. Despite heavy grazing pressure and potential damage from climate change, little is known about these peatlands. Our objective was to quantify carbon pools, basal ages and long-term peat accumulation rates in peatlands in two areas of the arid puna ecoregion of Bolivia: near the village of Manasaya in the Sajama National Park (Cordillera Occidentale), and in the Tuni Condoriri National Park (Cordillera Real).
- (2) We cored to 5 m depth in the Manasaya peatland, whose age at 5 m was *ca.* 3,675 yr. BP with a LARCA of 47 g m⁻² yr⁻¹. However, probing indicated that the maximum depth was 7–10 m with a total estimated (by extrapolation) carbon stock of 1,040 Mg ha⁻¹. The Tuni peat body was 5.5 m thick and initiated *ca.* 2,560 cal. yr. BP. The peatland carbon stock was 572 Mg ha⁻¹ with a long-term rate of carbon accumulation (LARCA) of 37 g m⁻² yr⁻¹.
- (3) Despite the dry environment of the Bolivian puna, the region contains numerous peatlands with high carbon stocks and rapid carbon accumulation rates. These peatlands are heavily used for llama and alpaca grazing.

KEY WORDS: Andes; LARCA; mountain; peat; puna

INTRODUCTION

The tropical mountains of Bolivia are part of the dry puna ecoregion that extends from central Peru south into the subtropics of northern Chile and Argentina. Despite the seasonally arid climate of the Bolivian Andes, they support a diverse array of wetlands including open aquatic beds, wet meadows and peatlands (Squeo *et al.* 2006). Peatlands are defined as wetlands that have accumulated thick horizons of organic matter (peat) and are regionally known as bofedales (Squeo *et al.* 2006, Cooper *et al.* 2010).

Peat forms because organic matter production is greater than decomposition. Although, globally, most peatlands are found in low-lying areas, especially in boreal or tropical (between 23.4° N and 23.4° S) regions, they also commonly occur in mountain ranges (Cooper *et al.* 2012) including the Andes of South America (Squeo *et al.* 2006, Chimner & Karberg 2008, Cooper *et al.* 2010, Benavides 2014). Bofedales are characterised by highly productive vegetation (Cooper *et al.* 2015) that is adapted to the

high-altitude Andes, and by water tables close to the soil surface, which may both be contributing factors to the development of thick peat deposits.

The Bolivian puna is characterised by a dry climate, which contrasts with the wetter tropical Andean ecoregions of the jalca in central Peru (Cooper *et al.* 2010) and the páramo that extends from northern Peru to Venezuela (Buytaert *et al.* 2011). The puna ecoregion is divided into three zones based on precipitation; the dry puna, the moist puna and the wet puna (Olson *et al.* 2001). The xeric climate of the puna does not seem favourable for peat formation, but Andean mountain peatlands have formed in locations that receive perennial inflows of groundwater recharged from a combination of seasonal rainfall and glacial and snow melt (Caballero *et al.* 2002, Chimner *et al.* 2010). Because of their reliance on these limited water supplies in an arid environment, they may be extremely vulnerable to changes in climate and land use that could alter peatland hydrology and reduce peat accumulation rates (Chimner & Cooper 2003, Cooper *et al.* 2015).

The high-altitude peatlands of the Bolivian Andes occur primarily at the bases of steep slopes, in mountain basins (especially behind moraines deposited by receding glaciers), or within wetland complexes on the altiplano, a large plateau bounded to the east by the Cordillera Real and to the west by the Cordillera Occidental. The majority are located in the alpine zone (3,200–5,000 m a.s.l.; Squeo *et al.* 2006). Peatlands in the puna range in size from a few hectares when confined by mountainous terrain to several square kilometres on the flat antiplano (Squeo *et al.* 2006).

Peatlands are an integral part of the global climate system due to their ability to sequester carbon dioxide and emit methane (Frolking *et al.* 2011). Globally, peatland ecosystems contain approximately 30 % of the terrestrial soil carbon (C) pool (Gorham 1991, Limpens *et al.* 2008). Tropical lowland peatlands are estimated to comprise 18–25 % of the global peat volume (Page *et al.* 2011), but the contribution of high-altitude Andean peatlands to C storage in the tropics is poorly quantified.

Because of the large uncertainty of tropical wetland C storage across the globe and in different wetland types (e.g., mangrove swamps, lowland peatlands, mountain peatlands) and the rapid rate of degradation of these ecosystems (Hooijer *et al.* 2010, Hergoualc'h & Verhot 2011, Kauffman *et al.* 2011, Koh *et al.* 2011), there are increased international efforts to gain a better understanding of tropical wetland C dynamics (Murdiyarsa *et al.* 2009). Large areas of tropical wetlands have been destroyed or seriously degraded, especially in lowland swamps (Hooijer *et al.* 2010). Peatlands in the Andean highlands are also experiencing high rates of land-use change due to increased resource demands (Salvador *et al.* 2014). They are often intensively used for livestock pasture by local communities because the highly productive wetland vegetation provides year-round green forage in an otherwise arid alpine landscape (Benavides *et al.* 2013, Cooper *et al.* 2015). Although grazing has occurred on Andean mountain peatlands for thousands of years, the type of grazing animals in the northern Andes has recently shifted from soft-footed native camelids (llamas and alpacas) to introduced hooved cattle and sheep, and the number of animals has increased across the Andes. In Bolivia, grazing occurs every day of the year without rest (Benavides & Vitt 2014, Urbina & Benavides 2015). The change in the type of grazers coupled with increasing herd sizes is affecting the sustainability of Andean peatlands (Salvador *et al.* 2014). Many of them are also damaged by mining, agriculture and hydrological alterations (Cooper *et al.* 2010, Salvador *et al.* 2014).

In addition to land-use changes, climate change is a growing concern for the long-term stability of peatland ecosystems in the Andes (Urrutia & Vuille 2009). The 2–7 °C increase in mean annual temperature predicted for the Bolivian highlands by the end of the 21st century will potentially alter regional precipitation patterns and evapotranspiration rates (Bradley *et al.* 2004). Increased mean annual temperatures in the Andes are already causing high rates of glacial recession and loss of snow pack (Ramírez *et al.* 2001, Vuille *et al.* 2003).

Despite long-term net peat accumulation, the delicate balance between plant production and decomposition in peatlands favours peat formation only under perennially anoxic soil conditions. Alteration of the vegetation and reductions in water availability can quickly transform a peatland from a C sink to a C source, impairing its ecological integrity (Limpens *et al.* 2008). This environmental threshold is already closely approached in water-stressed arid regions such as the Bolivian puna.

Because climatic and anthropic pressures could threaten the ability of tropical mountain peatlands in Bolivia to function as long-term C sinks, it is important to obtain baseline data on C dynamics as a reference for current and future assessments of bofedal health, sustainability and regional C storage. Therefore, the objective of our research was to quantify C pools and long-term peat accumulation rates in two Bolivian tropical mountain peatlands.

METHODS

Study sites

This study was conducted at two sites within the puna ecoregion of north-western Bolivia. We sampled peatlands near the village of Manasaya in the Cordillera Occidental within Sajama National Park, and in the Cordillera Real within Tuni Condoriri National Park. The peatlands are hereafter referred to as Manasaya and Tuni, respectively (Figure 1). Manasaya (Figure 2) is at an altitude of 4,496 m a.s.l. and Tuni (Figure 3) is at 4,615 m a.s.l. Manasaya (18° 04' 08" S, 69° 02' 00" W) contains dense, mineral-rich peat and is suggested to have formed as primary peat on mineral soils. In contrast, Tuni (16° 13' 06" S, 68° 13' 21" W) has highly organic peats that formed on top of lake sediments. Manasaya is within the dry puna on the western side of the Andes, with mean daily temperature 4.6 °C and annual precipitation only 321 mm yr⁻¹ (Beck *et al.* 2010). Tuni is within the wet puna on the eastern side of the Andes, where mean daily temperature is similar at 4.6 °C but precipitation is approximately 700 mm yr⁻¹ (EPSAS 2009).

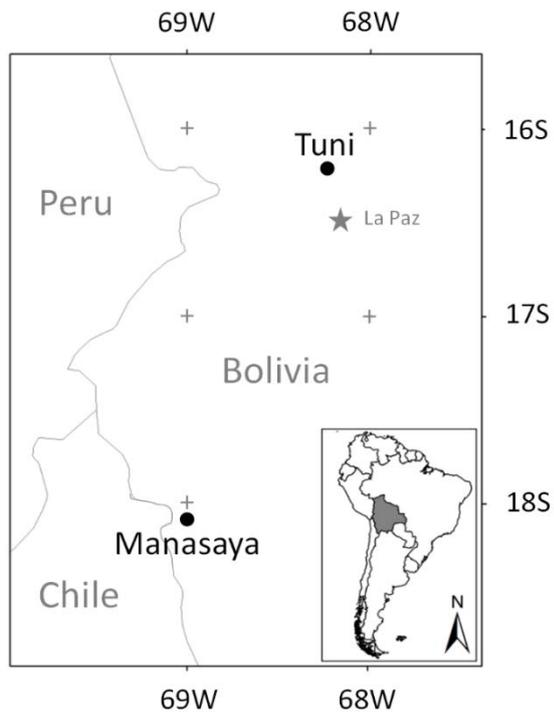


Figure 1. Map of north-western Bolivia showing the locations of the Manasaya and Tuni study sites (black dots).

The two study sites are dominated by the cushion plants *Distichia muscoides* Nees & Meyen and *Oxychloe andina* Phil. At Manasaya, *Deyeuxia spicigera* J. Presl and *Distichia filamentosa* Buchenau are also common. Other common species at Tuni are *Deyeuxia rigescens* (J. Presl) Türpe and *Plantago tubulosa* Decne. Tuni has an overall slope of 1–4 % and Manasaya is slightly more inclined with a slope of 2–5 %. Both of these peatlands are fens supported by groundwater discharge from local hillslope aquifers that are recharged by rain and snowmelt water.

Depth to the water table was measured in fully slotted groundwater monitoring wells from October 2012 through March 2014. The Manasaya water table, measured near the coring location, remained within 15 cm of the soil surface during the entire measurement period. In other portions of this peatland the water table was near the soil surface during the rainy season but fell to 20–40 cm depth for weeks or months at a time during the dry season (March through October). The pH of groundwater at Manasaya averaged 6.5. The water table at Tuni was within 15 cm of the soil surface throughout the study period, and the pH averaged 5.0.



Figure 2. The Manasaya peatland, Sajama National Park. Its vegetation consists of large circular green masses of *Distichia muscoides* surrounded by *Deyeuxia spicigera*, other grasses and sedges.



Figure 3. The Tuni peatland, which lies within the Tuni Condoriri National Park, Cordillera Real.

Peatland surface and basin morphology

We characterised the surface and basin morphology of the peatlands in October 2012. We established a series of transects in each peatland and used an extendible steel 'tile probe' (usually used to locate underground pipes) to measure the approximate depth to mineral soil. Mineral soil was identified from an increase in resistance to downward movement of the probe or from scratching of the probe on sand or rocks. The ground surface at each probed point was surveyed with a survey-grade GPS unit (Model HiPer[®] Lite+, Topcon Positioning Systems Inc., Livermore, CA, USA). We were thus able to calculate the ground surface altitude as well as the approximate altitude of the underlying mineral surface. These datasets allowed us to create maps and valley cross-section profiles of the two surfaces; and to calculate peatland surface area, mean thickness, and volume.

Soil core sampling and carbon analyses

A single core was extracted from each of the two sites. The upper 50 cm of each peatland was cored with a 10 cm diameter × 50 cm long polyvinyl chloride (PVC) corer constructed by cutting a 50 cm long thin-walled (3.2 mm) PVC pipe longitudinally

and then assembling the two halves with metal H-channel that ran the length of the pipe. The corer was secured with four metal band clamps equally spaced along the length of the corer. The first 20 cm of the corer was inserted carefully into the peat by cutting around the perimeter of the pipe with a sharp serrated knife as the pipe was lowered, to prevent compaction of the surface peat. The remaining 30 cm of the corer was pounded into the peat with a rubber mallet. Deeper core sections (> 50 cm) were sampled with a Russian pattern peat borer (D-pattern corer with a 5 cm diameter by 50 cm long sample chamber; Aquatic Research Instruments, Hope, ID, USA) until the base of the peat was encountered or we were unable to push the borer any deeper into dense, mineral-rich peats. We used a two-borehole technique with boreholes approximately 50 cm apart. Once collected, the peat samples were cut into 10 cm sections in the field. Core sections were immediately placed in small plastic ziplock bags, labelled with 'top' and 'bottom' to preserve shape and orientation, and transported to Michigan Technological University.

In the laboratory, core sections were dried in a convection oven at 65 °C until a constant mass was obtained. Dry bulk density (g cm^{-3}) for each 10 cm

section was calculated by dividing the oven-dried soil mass by the original sample volume determined from the corer volume. The core sections were then cut longitudinally, one half archived for future macrofossil analysis and the other half cut into approximately 5 cm long samples for carbon (C), nitrogen (N), and loss on ignition (LOI) analyses. The 5 cm samples were then ground and homogenised to a fine powder with a ball mill (SPEX 8000M, Metuchen, NJ, USA), re-dried to constant mass at 65 °C, and stored in airtight plastic vials. Organic matter proportion was determined on an approximately 1 g subsample of the ground sample for all core sections by LOI at 550 °C for four hours (Chambers *et al.* 2011). Subsamples were also analysed for C and N with an elemental analyser (Costech 4010, Valencia, CA, USA and Fisons NA 1500, Lakewood, NJ, USA).

A linear regression between LOI and C was used to provide a cheaper surrogate for C analysis of peat soils. The equation was derived from the entire Manasaya and Tuni core dataset of 210 soil samples taken at 5 cm intervals, and resulted in a highly significant regression ($P < 0.0001$; $R^2 = 0.992$) between LOI (%) and C (%):

$$C = 0.5641 \text{ LOI} - 0.4167 \quad [1]$$

Carbon density (mg cm^{-3}) for each core section was calculated as the product of its dry bulk density, length of core section, and % C. The total peatland C storage (Mg = metric tonne) was estimated as the product of the peatland's volume (estimated from probing) and its mean C density, calculated for the samples in the two cores. Peatland C storage was reported on a *per* area basis (Mg ha^{-1}) by dividing the total C stock by the surface area (ha) of the peatland. This was done both assuming an unsloped basin (peat volume not corrected for the basin shape of the peatland - the result typically reported in most coring studies) and using the measured peat volume (based on actual basin morphology determined by probing). For the C density estimates used for extrapolation to greater depths and to basin scale, we used the mean C density from the whole core (Chimner *et al.* 2014). Thus, for the Manasaya core we extrapolated to the 10 m probing depth using the mean C density estimate for the whole 5 m core. We report both the Manasaya conservative estimate for 5 m cored depth and the extrapolated estimate for the 10 m probed depth.

Peatland age and accumulation rates

Soil samples from the base of the peatland and samples from multiple depths in each peat column

were analysed for bulk ^{14}C dating. Peat for dating was extracted from the interiors of the unground core sections to prevent contamination from the surface of the sample. Bulk soil samples were graphitised in preparation for ^{14}C measurement at the Carbon, Water & Soils Research Laboratory at Michigan Technological University in Houghton, Michigan. After grinding, samples were dried, placed into quartz tubes with cupric oxide (CuO) and silver (Ag), sealed under vacuum, and combusted at 900 °C for six hours to form CO_2 gas. The CO_2 was then reduced to graphite by heating at 570 °C in the presence of hydrogen (H_2) gas and an iron (Fe) catalyst (Vogel *et al.* 1987). Graphite targets were then analysed for radiocarbon abundance using an accelerator mass spectrometer (Davis *et al.* 1990) at Lawrence Livermore National Laboratory and corrected for mass-dependent fractionation using measured $\delta^{13}\text{C}$ values according to Stuiver & Polach (1977). The radiocarbon dates were calibrated to calendar dates (cal. yr. BP, BP = 1950) (Stuiver & Reimer 1993, version 5.0) using a southern hemisphere correction curve (McCormac *et al.* 2004). The *ca.* modern ^{14}C date from the Tuni core depth of 40–50 cm was calibrated with CALIBomb (Hogg *et al.* 2013) using a southern hemisphere correction (Hua *et al.* 2013). The median value of the 2σ calibration range for each date was reported and used in calculating accumulation rates.

The long-term apparent rates of C accumulation (LARCA, $\text{g m}^{-2} \text{yr}^{-1}$), soil mass accumulation ($\text{kg m}^{-2} \text{yr}^{-1}$), and peat depth accumulation (mm yr^{-1}) for each peatland were determined from the line slopes (not forced through zero) of each variable plotted *versus* the ^{14}C dates. The LARCA is a common method of assessing long-term peat accumulation (Clymo *et al.* 1998). In short, it calculates the rate of C accumulation by dividing the mass *per* unit area of C by the age of the peatland. This method is simple, but must be used with care because it calculates only the apparent rate of C accumulation and does not account for decay after the peat was formed. Because of this limitation, caution must be exercised when comparing the LARCA values of peatlands with different ages.

RESULTS

At Manasaya, dense peat soils allowed coring to only 500 cm with our equipment. Probing indicated that the peat was approximately 10 m thick at the core location (Table 1). Our deepest dated sample was at 440–450 cm and had an age of 3,471 cal. yr. BP (Table 2). The height *versus* age profile (Figure 4)

Table 1. Core depth, peat thickness, basal age, C stock, peat properties (dry bulk density (D_b), carbon density (D_c), loss on ignition, LOI (%), C (%), N (%) and mean C/N value for entire core); and long-term rates of growth in carbon (LARCA; $\text{g m}^{-2} \text{yr}^{-1}$), peat thickness (mm yr^{-1}) and mass ($\text{kg m}^{-2} \text{yr}^{-1}$) for the Manasaya and Tuni sites.

	Manasaya	Tuni
Core depth (cm)	500*	550
Peat thickness (cm)*	1000	550
Core basal age (cal. yr. BP)	3675 [†]	2230
Carbon stock (Mg ha^{-1})	1040	572
<i>Peat properties</i>		
Dry bulk density, D_b (g cm^{-3})	0.17	0.05
Carbon density, D_c (mg cm^{-3})	35.8	21.5
Organic matter, LOI (%)	42.8	85.6
C (%)	23.9	47.8
N (%)	1.1	2.0
C/N	20.9	23.8
<i>Accumulation rates</i>		
LARCA ($\text{g m}^{-2} \text{yr}^{-1}$)	47	37
Rate of peat growth (mm yr^{-1})	1.4	2.2
Rate of mass growth ($\text{kg m}^{-2} \text{yr}^{-1}$)	0.22	0.08

*The Manasaya core does not represent the full thickness of the peat, which was estimated by probing to be ~ 10 m.

[†]Peatland initiation date was estimated at *ca.* 7,300 yr. BP by extrapolation from the calculated cumulative soil thickness equation with the assumption that it remained linear throughout the portion of the peatland not sampled.

was used to extrapolate linearly to the 500 cm core (i.e., assuming a linear relationship) and gave the deepest sample collected (still apparently several metres above the base of the peatland) an estimated date of *ca.* 3,675 yr. BP.

The top 500 cm of the Manasaya peatland had a long-term peat accumulation rate of 1.4 mm yr^{-1} and a soil mass accumulation rate of $0.22 \text{ kg m}^{-2} \text{yr}^{-1}$, with a LARCA of $47 \text{ g m}^{-2} \text{yr}^{-1}$ (Figure 4). All accumulation rates were calculated from nine calibrated dates distributed through the top 450 cm of the core (Figure 4 and Table 2). The core had a mean

soil dry bulk density of $0.17 \pm 0.07 \text{ g cm}^{-3}$ (± 1 SD), a mean peat C proportion of $24 \pm 8 \%$ (Figure 5), and a mean soil organic matter proportion of $43 \pm 16 \%$. The core contained a total of 40 cm of embedded mineral-rich horizons that were $< 12 \%$ C at depths of 50–60, 80–90 and 360–380 cm below the surface. The mean C density was $36 \pm 11 \text{ mg cm}^{-3}$ and $29 \pm 7 \text{ mg cm}^{-3}$ for the peat and the mineral layers, respectively. The entire core had a mean soil C density of $36 \pm 11 \text{ mg cm}^{-3}$ (Figure 5). Scaling up from the single-core C measurements to an areal basis (without considering basin morphology) gave the peatland a C storage of $1,790 \text{ Mg ha}^{-1}$ at the conservative 500 cm depth, and $3,580 \text{ Mg ha}^{-1}$ when extrapolated to the probed 10 m depth using the mean C density of the whole 500 cm core. The mean peat thickness determined from the probing survey was 470 cm, translating to $280,130 \text{ m}^3$ of peat (Figure 6). Applying the mean C density from the whole core (36 mg cm^{-3}) to the volume of peat in the basin indicated a total-peatland C storage of 10,025 Mg. Adjusting the total-basin C storage to the peatland surface area of 9.64 ha resulted in a total C storage on a *per area* basis of $1,040 \text{ Mg ha}^{-1}$.

The Tuni peat core was 550 cm long and the peatland was on top of several metres of lake sediment. At a depth of 300–350 cm below the peat surface a layer of water was encountered (Figure 5). The basal date of the peatland was 2,563 cal. yr. BP. The long-term peat accumulation rate was 2.2 mm yr^{-1} and $0.08 \text{ kg m}^{-2} \text{yr}^{-1}$, with a LARCA of $37 \text{ g m}^{-2} \text{yr}^{-1}$ (Figure 4). All accumulation rates were calculated from ten calibrated dates distributed throughout the core (see Figure 4 and Table 2). The entire core was peat ($> 12 \%$ C) with no embedded mineral soil horizons and had a mean dry bulk density of $0.05 \pm 0.02 \text{ g cm}^{-3}$ (Figure 5). The mean peat C proportion was $48 \pm 6 \%$ with a mean organic matter proportion of $86 \pm 11 \%$. Mean C density of the entire core was $21 \pm 8 \text{ mg cm}^{-3}$ (Figure 4). Scaling up from the single-core C measurements to an areal basis gave the peatland a total C storage of $1,075 \text{ Mg ha}^{-1}$. The probing survey across the entire peatland determined that the mean peat thickness was 200 cm and the peatland contained $18,356 \text{ m}^3$ of peat (Figure 7). Applying the mean C density from the whole core of 21 mg cm^{-3} to the volume of peat in the basin produced an estimate of total peatland C storage of 395 Mg. Adjusting the total basin C storage to the peatland surface area of 0.69 ha resulted in a total C storage on a *per area* basis of 572 Mg ha^{-1} .

Carbon and nitrogen results are reported in Figure 5, but will be considered in a separate regional synthesis.

Table 2. Radiocarbon ages (^{14}C) corrected for mass-dependent fractionation using measured $\delta^{13}\text{C}$ and calibrated ages (cal. yr. BP) for the Manasaya and Tuni cores. Median value of the 2σ calibration range for each calibrated date is reported.

	*CAMS #	Depth (cm)	$\delta^{13}\text{C}$	^{14}C age	\pm	cal. yr. BP	median -2σ	median $+2\sigma$
	168472	50–55	-25.10	675	25	604	558	652
	164923	90–100	-26.70	1195	30	1034	965	1109
	164924	140–150	-26.10	1490	25	1335	1301	1372
	164925	190–200	-26.40	1545	25	1380	1312	1431
Manasaya	164926	240–250	-26.30	1790	25	1652	1589	1716
	164927	290–300	-26.40	1810	25	1660	1605	1740
	164928	340–350	-27.10	2055	30	1964	1893	2021
	164929	390–400	-27.10	2985	25	3099	2990	3183
	164930	440–450	-26.50	3290	25	3471	3396	3561
	164729	40–50	-24.71	25	25	1955 [†]	1955 [†]	1956 [†]
	161015	95–100	-25.36	190	30	179	134	285
	161016	140–145	-25.26	405	30	430	430	498
	161017	200–205	-25.24	865	25	729	680	770
	161018	235–240	-25.74	920	25	774	729	807
Tuni	161019	285–290	-26.00	1160	35	1015	934	1073
	161020	360–365	-25.54	1385	25	1278	1260	1305
	161021	395–400	-25.71	1575	30	1414	1354	1519
	161022	450–455	-25.63	1910	25	1801	1735	1876
	161023	500–505	-25.75	2230	25	2230	2147	2312
	161024	545–550	-24.91	2505	25	2563	2378	2623

*The CAMS# is the sample reference number from the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory.

[†]Values expressed in cal. yr. AD due to the fact that the sample could be younger than 1950 AD. One sigma values were selected for this sample using the age of the peat below to constrain the most probable age of the stratum.

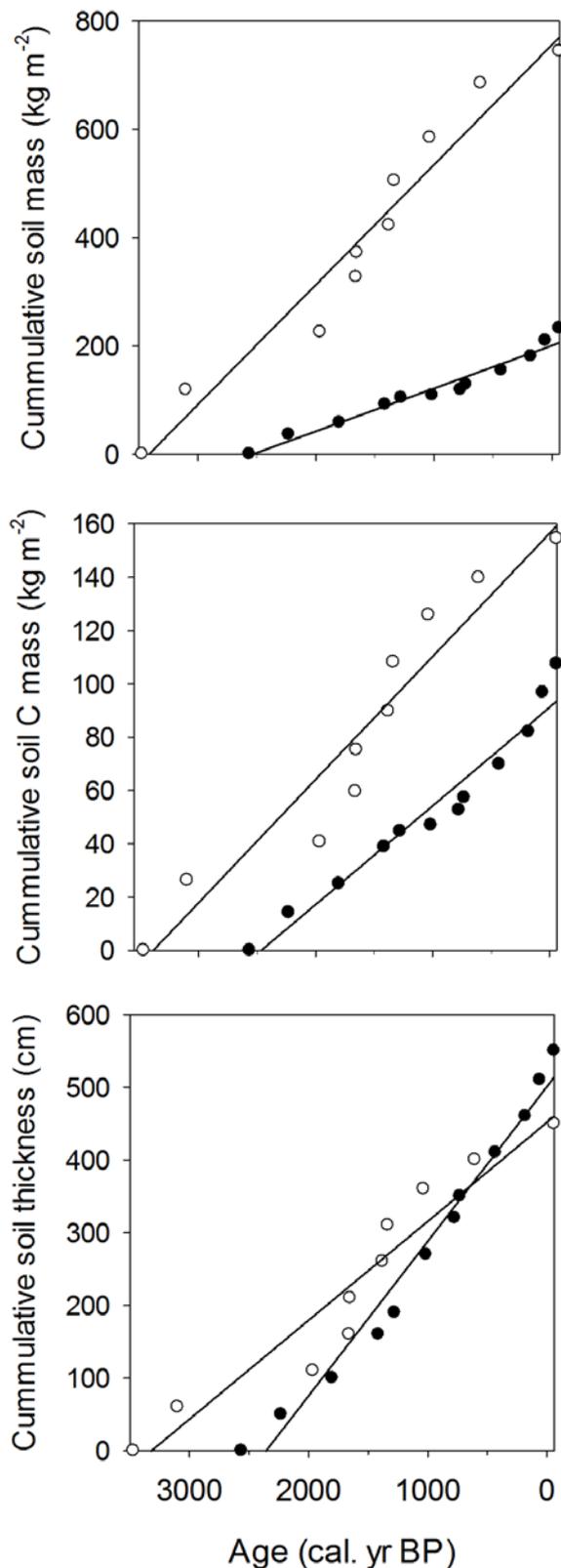


Figure 4. Cumulative soil mass (kg m^{-2}), carbon mass (kg m^{-2}), and thickness (cm) of the dated cores (cal. yr. BP) from the Manasaya (unfilled circles) and Tuni (solid circles) peatlands. Lines are best fit (minimised sum of squares of differences) straight lines.

DISCUSSION

The peatland C stocks measured from our cores and scaled to a *per* area basis for Manasaya and Tuni (3,580 and 1,075 Mg ha^{-1} respectively) are similar to or even larger than other tropical mountain peatland C stocks measured in the more humid and wetter climates of the Peruvian jalca (Cooper *et al.* 2010) and the Ecuadorian páramo (Chimner & Karberg 2008, Hribljan *et al.* unpublished data). Using the same calculation method, North American temperate mountain peatlands contain, on average, 1,200 Mg C ha^{-1} (Chimner 2000, Cooper *et al.* 2012). However, these other C stock estimates are calculated from single cores, often taken in the deepest part of the peatland. Our extensive probing at Manasaya and Tuni allowed us to estimate the entire peatland basin volume, and thus obtain a better estimate of total C storage per hectare. The peatland C estimates that take into account basin morphology for Manasaya (1,040 Mg ha^{-1}) and Tuni (572 Mg ha^{-1}) are 53 % and 29 % less than the estimates extrapolated from the single cores. These differences arise from the bowl-shaped morphology of these mountain peatlands. The difference is most pronounced at Manasaya (Figure 6), which has a more gradually sloping basin compared to Tuni (Figure 7) with a steeply sloping basin. However, despite the corrections for basin morphology, these tropical mountain peatlands in the dry puna ecoregion of Bolivia still contain large pools of soil C on an area basis.

Locating the bottoms of peatlands by probing can be uncertain in some sites due to embedded mineral layers and substratum sediments. Lake sediments, which are difficult to differentiate from peat during probing, are commonly found upslope of glacial moraines or restrictions in the valley topography formed by tectonic or volcanic activity, or by alluvial fan formation that can impound water. The Tuni peatland formed on a lake bed *ca.* 2,563 cal. yr. BP. We did not encounter solid substratum by probing until 10 m below the peatland surface at the deepest probed locations due to the presence of a thick layer (4.5 m) of lake sediments. Uninformed probing could mistake lake sediment for peat, and thus overestimate peat thickness at Tuni or similar sites. However, it should be noted that the deep lake sediments below the Tuni peatland contribute an additional 350 Mg C ha^{-1} based on our sampling. This is an important but often ignored stock of C in mountain basins.

In contrast to the Tuni site, our data indicate that lake sediments were not present under the cored area at Manasaya. However, we were unable to confirm the presence of peat or the absence of lake sediments

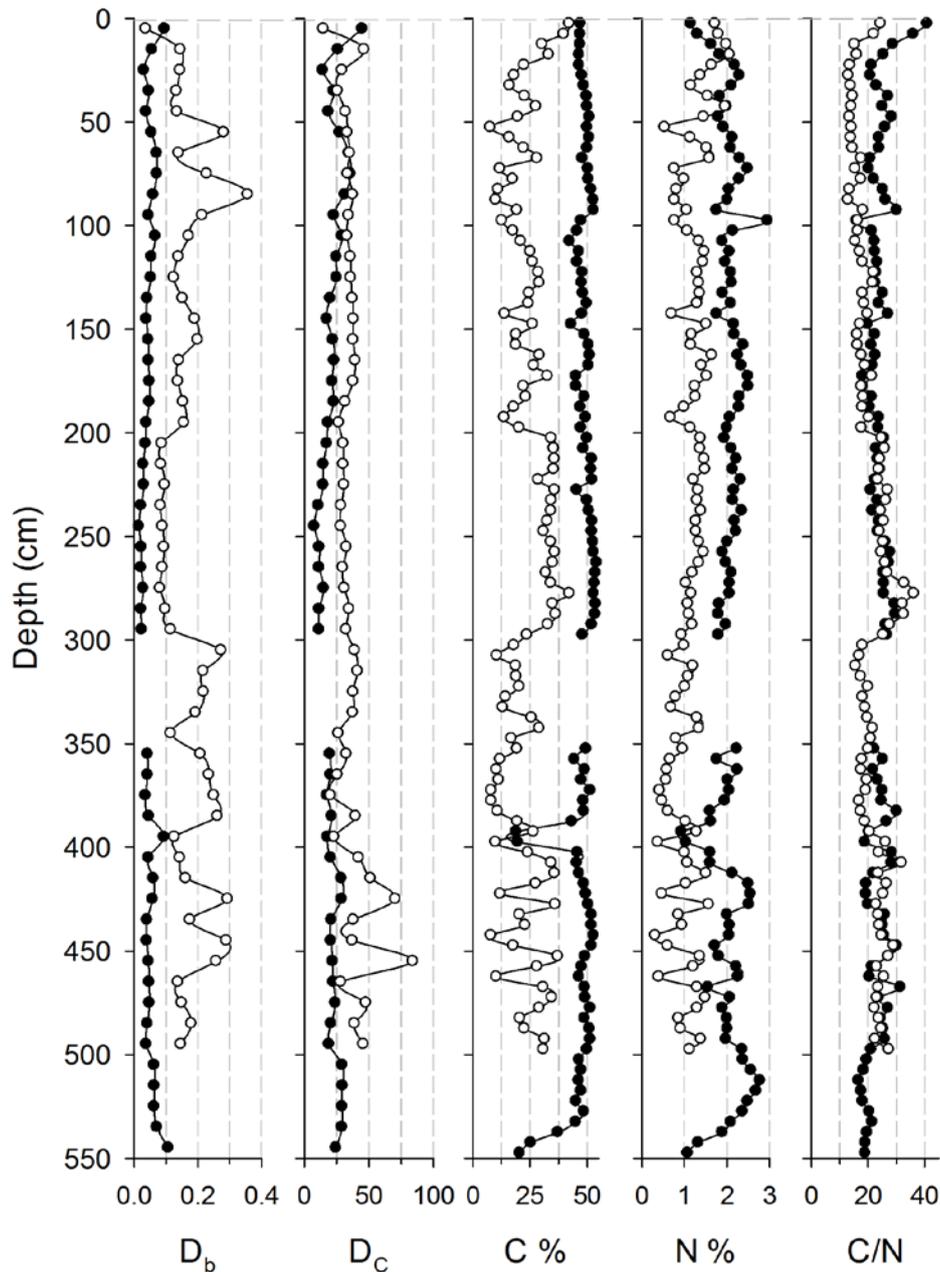


Figure 5. Soil dry bulk density (D_b ; g cm^{-3}), carbon density (D_c ; mg cm^{-3}), carbon concentration (C %), nitrogen concentration (N %), and C/N quotient for the Manasaya (unfilled circles) and Tuni (solid circles) peat cores.

in these deeper soil layers because of our inability to core beyond 5 m. The peatland has a sloping unconstrained basin unlike the constrained bowl-shaped basin of the Tuni site, suggesting that the peatland was initiated through primary peat formation where groundwater discharges to the soil surface in the valley bottom rather than on lake sediments. In support of this model, glacial moraines or valley restrictions that could contribute to pond formation were not evident downslope of this

peatland. Probing at Manasaya encountered coarse mineral sediment under the peat, and hence is unlikely to over-estimate peat depth.

The large C storage in these Bolivian tropical mountain peatlands is surprising given the xeric climate of the puna ecoregion. The wet puna ecoregion can have similar annual mean precipitation to the wetter jalca and páramo ecoregions. However, the puna climate is less humid and more seasonal, receiving the rainfall over a shorter wet season, and

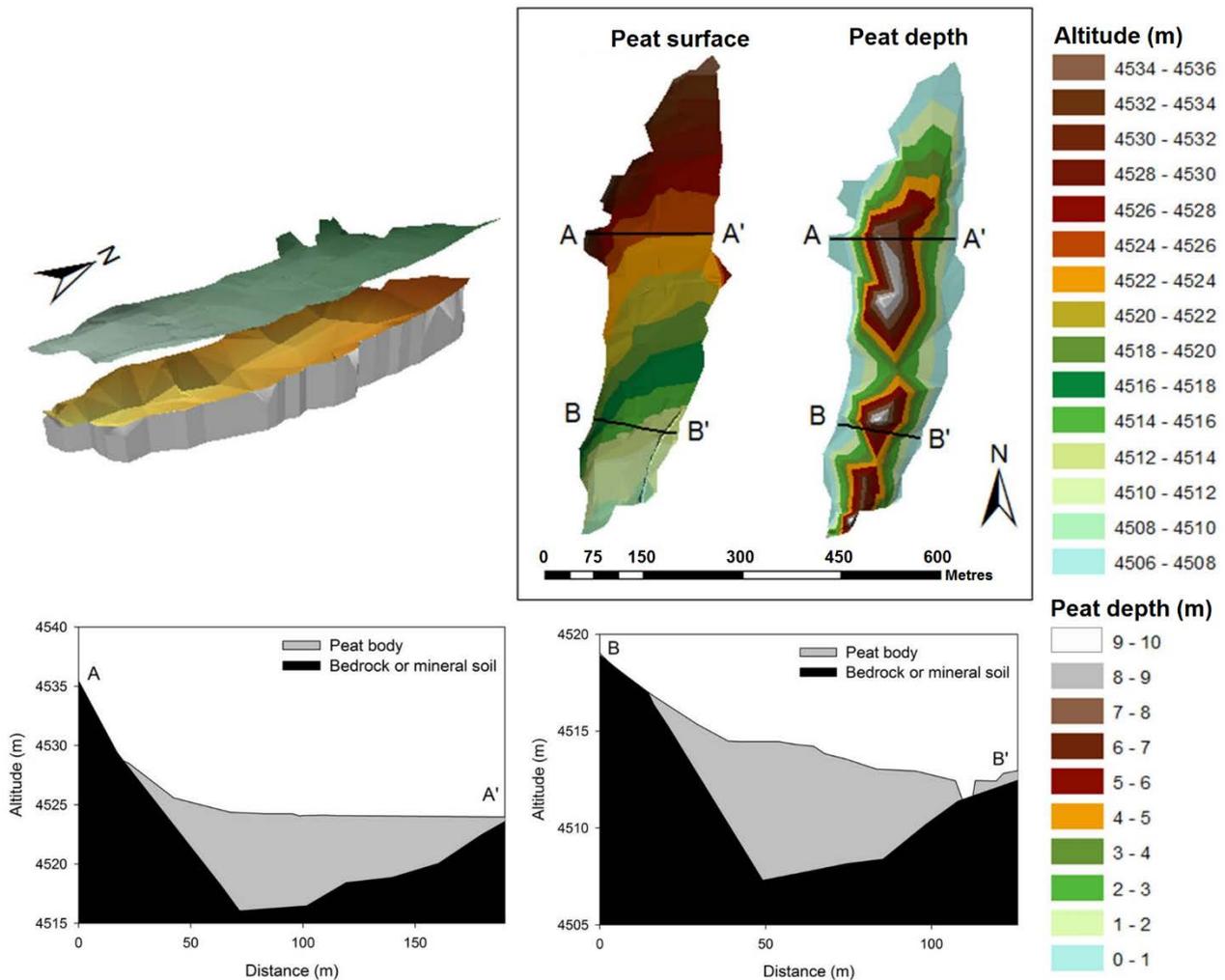


Figure 6. Diagrams of the Manasaya peatland depicting basin morphology, surface altitudes, and thickness of the peatland. The bottom two diagrams are cross-section views of the peatland from locations indicated in the upper right diagram.

can be extremely arid for more than half of the year. Nevertheless, our data demonstrate that puna peatlands are able to rapidly accumulate deep peat deposits despite the seasonally arid conditions. The peatlands are probably able to maintain saturated soil conditions due to hillslope infiltration of precipitation and snowmelt that recharges the local water table and discharges into the peatlands throughout the year (Caballero *et al.* 2002). In addition, the deep rooting zone of the cushion plants (Fritz *et al.* 2011) could provide a means to access water deeper in the peatland during dry seasons. However, because these peatlands are highly reliant on capturing a limited water supply, they are vulnerable to any changes in regional climate and local hydrology.

The peat we sampled at Manasaya and Tuni showed contrasting mineral contents. The Manasaya

peatland had dense mineral-rich peat whereas the highly organic peat at Tuni contained, on average, less than 15 % mineral material. The Manasaya peat seems to have formed in conjunction with mineral deposition from aeolian processes and alluvial movement of sediment from steep hillslopes onto valley bottoms. In other regions of the Andes, volcanic eruptions can contribute to the formation of dense peat by depositing substantial amounts of tephra onto peatlands (Chimner & Karberg 2008, Benavides *et al.* 2013, Hribljan unpublished data). However, our area remained volcanically inactive during the time of peat formation and contained no volcanic deposits. In contrast to Manasaya peat, Tuni peat was composed of primarily organic material with little inorganic mineral content, despite being bordered by steep talus slopes with loose scree. The

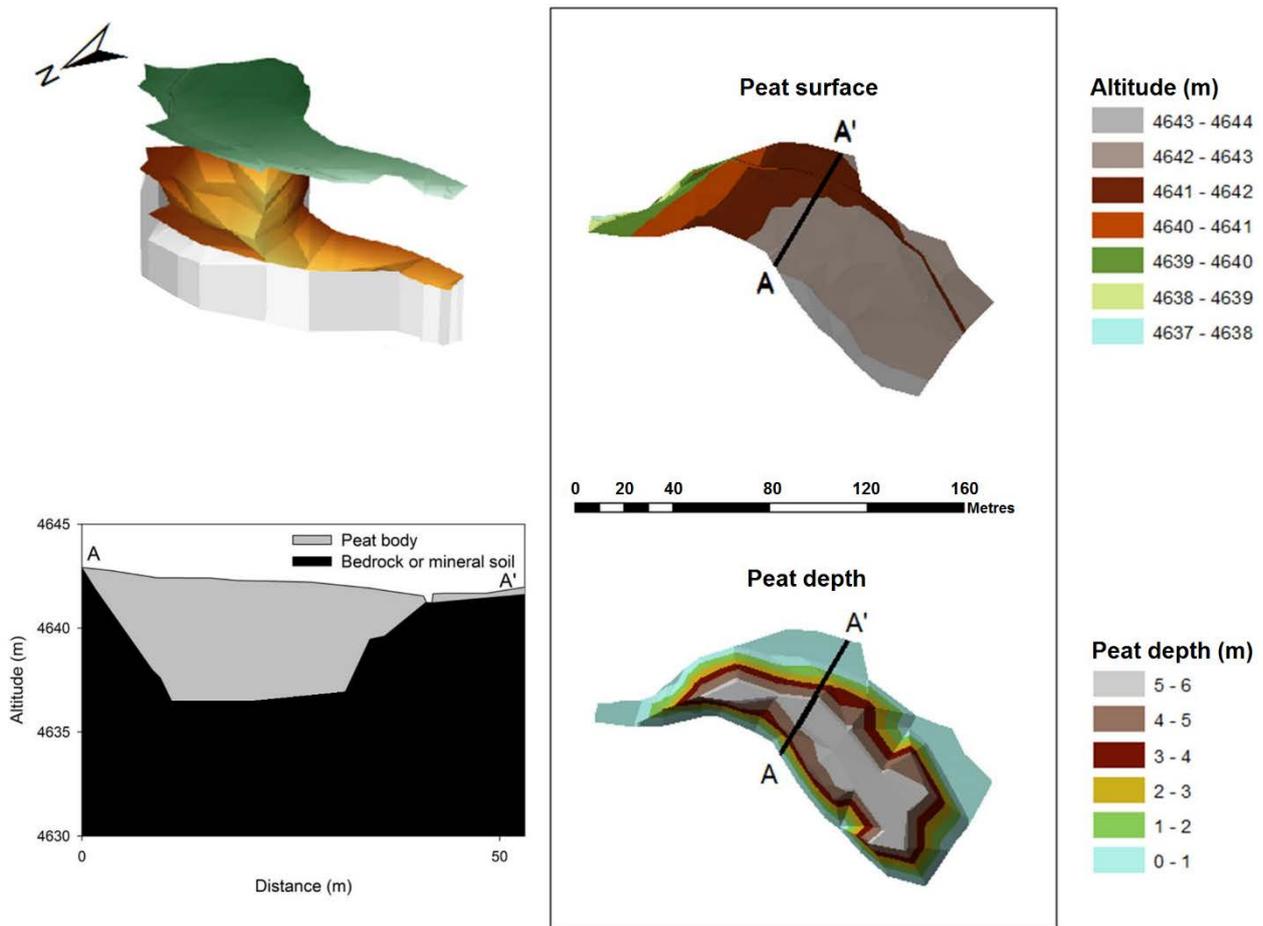


Figure 7. Diagrams of the Tuni peatland depicting basin morphology, surface altitudes, and thickness of the peatland. The bottom left diagram is a cross-section view of the peatland from a location indicated in the right diagram.

mineral-rich Manasaya peatland had a higher LARCA than the organic-rich Tuni peatland, suggesting that the differences in mineral proportion between the Manasaya and Tuni cores could be indicative of (or contributory to) higher rates of C accumulation. More extensive sampling is required to determine whether this is a general phenomenon.

Despite the differences in peat mineral proportion, both peatlands had rapid accumulation rates. Our calculated long-term accumulation rates of 1.4 mm yr⁻¹ for Manasaya and 2.2 mm yr⁻¹ for Tuni were 5–9 times faster than the 0.25 mm yr⁻¹ average mean peat accumulation rate for North American mountain peatlands reported by Cooper *et al.* (2012). Thus, the peatlands we investigated in the Bolivian highlands have accumulated large C stores in a relatively short period of time. Manasaya and Tuni have LARCA of 47 and 37 g m⁻² yr⁻¹ respectively, and in this regard are similar to peatlands in the

wetter Ecuadorian páramo which have LARCA of 12–50 g m⁻² yr⁻¹ (Chimner & Karberg 2008, Hribljan unpublished data). These rates are somewhat higher than those of North American mountain peatlands, which have an average LARCA of 25 g m⁻² yr⁻¹ (Chimner 2000). Thus, Bolivian peatlands have accumulated C more rapidly than most other mountain peatlands in the world, at rates similar to C accumulation rates (39–85 g m⁻² yr⁻¹) measured in tropical lowland peatlands (Lähteenoja *et al.* 2009).

Initiation of the two peatlands appears to have occurred between 2,500 and 7,300 years ago. We have high confidence that the basal age at Tuni was *ca.* 2,563 cal. yr. BP because of the clear transition to non-peat lake sediments. Manasaya may be older than the *ca.* 3,675 years calculated for 500 cm depth from our core. We probed to 10 m in the thickest parts of this peatland before contacting a coarse substratum, and lake sediment was not likely at this

site. Extrapolating age linearly to the estimated 10 m depth would give a peatland initiation date of *ca.* 7,300 yr. BP, which coincides with a wet climatic period *ca.* 7,500–6,500 yr. BP (Tapia *et al.* 2003). However, this extrapolation is tentative because it assumes a linear height *versus* age profile, and we do not know if the depth determined by probing included substratum sediments or if there was a shift in the long-term peatland height accumulation rate prior to 3,675 yr. BP that would change our estimate of initiation date.

Tuni was initiated more recently than Manasaya, approximately 1,000 years into a wetter period that began *ca.* 3,500–3,000 BP following a drier period that began around 6,000 yr. BP (Thompson *et al.* 1998, Tapia *et al.* 2003). The lag in peatland initiation at Tuni could reflect lake basin dynamics, the peatland forming on the lake margin then infilling the basin. This interpretation was supported by the lake sediments we found below the peat. At Manasaya the response to a wetter climate could be more immediate because there is no evidence of a lake basin, so that peat could begin to form in areas of groundwater discharge. Thus, in both cases the estimated date of initiation was consistent with the hypothesis that the peatland is sensitive to climate change that affects the regional water balance.

Although mountain peatlands in the puna ecoregion are small compared with many northern peatlands and tropical lowland peat swamp forests, they are numerous across the highlands of southern Peru, Bolivia and northern Chile (Earle *et al.* 2003, Squeo *et al.* 2006, Maldonado Fonkén 2014, Salvador *et al.* 2014) and thus likely to represent a substantial regional C pool. However, despite the long-term accumulation of C in Bolivian mountain peat soils, these ecosystems are under intensive use by domesticated camelids and are vulnerable to multiple disturbances that threaten their sustainability. Therefore, it is critical to gain an improved understanding of their spatial distribution, basin morphology, peat soil variability, and current ecosystem C fluxes. Developing strong baseline data on their C dynamics will allow accurate scaling of C stocks and prediction of the future trajectory of C dynamics, providing a more informed estimate of the contribution of Andean peatlands to global C cycling. Because long-term sustainability of ecosystem services is needed to support pastoral communities in the Andes, the future management of high-altitude Andean peatland ecosystems must aim to achieve balance in preserving their hydrological integrity, their productivity, and the many services (i.e. biodiversity, C storage, pasture, and water supply) that they provide.

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